

Growth of Vegetative Organs in Water Chestnut, (*Trapa bispinosa* Roxb.)

Susumu ARIMA, Noriyuki TANAKA and Fumitake KUBOTA*

(Laboratory of Crop Science)

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Summary

This investigation was conducted to clarify the time, position and order of emergence of vegetative organs on water chestnut (*Trapa bispinosa* Roxb.) cultivated in a paddy field and to observe the forms of organs and their growing process.

1. The hypocotyl elongated spirally toward the surface of the water and had about 150 branch roots. The deeper the water, the growth of the root system of hypocotyl became vigorous. The branch roots showed heterorhizy and the ones that emerged from the basal part of a hypocotyl pierced the soil of the bottom and turned into underground roots. The roots, which were emerged between the basal part and the end of the hypocotyl, turned into water roots that were floating in the water.

2. Four stems emerged from a cotyledon node. Each stem had a fixed position and order of emergence. The stem which emerged earlier grew more vigorously than those emerged later.

The stem formed nodes at the shoot apex with regular intervals throughout the whole growth period. The rate of node forming was over 1.5 nodes per day during the middle stage of growth (high temperature period) and it was under 1.0 node per day during the earlier and later stages (low temperature periods). One leaf, a pair of water roots, more than ten underground roots and one bud emerged from a fixed position of node. During the reproductive stage one flower bud instead of a branch bud emerged from every several nodes.

The branch buds which emerged by the early flowering stage elongated from every several nodes and formed a rosette on the surface of the water. The branched stems showed the same growing pattern as the mother stem. The highest branching order was fifth, but the higher order branches often fell off halfway through the growing process.

The stem showed different growth habits before and after the beginning of flowering. During the vegetative stage it had elongation growth and at the reproductive stage it had thickening growth.

3. The leaf showed heterophylly with different forms according to its growth stage and environmental conditions. In this report we classified the water leaves into two kinds and the floating leaves into four kinds based on their morphological features.

4. The number of rosettes became highest at the end of July and they covered completely the surface of the water. When the leaf community had a high density of rosette, the floating leaves turned into emerged leaves and formed a three-dimensional productive structure on the surface of the water.

5. At the reproductive stage, each rosette was composed of about 40 floating leaves. From

* Faculty of Agriculture, Kyushu University

the middle of August to the beginning of September when all the leaves turn into adult leaves, the leaf area of the rosette became largest. But in the middle of September, with autumnal coolness, the rate of leaf-emergence was slower down and the new leaves became smaller and smaller in size. As a result, the leaf area gradually became smaller.

6. In October, the color of the leaf-blade turned brown and the leaves began to fall off from the ones which were near the circumference of the rosette. In November, the rosette disappeared with the stems and roots remaining in the water, but soon both of them decayed.

Key words: water chestnut (*Trapa bispinosa* Roxb.), aquatic plant, vegetative organ, heterophylly, heterorhizy.

Introduction

Water chestnut is an aquatic herb which is widely distributed in Europe, Africa and Asia. It is considered as a useful plant because it has fruit with starch of fine quality. It is widely cultivated in India, Indonesia, the southern part of China, Italy, etc^{1, 2)}. In Japan it is also cultivated in the Chikugo plain of Kyushu, and recently *Trapa bispinosa* Roxb. with non-spine and big grains has been cultivated in paddy fields³⁾.

Water chestnut is classified as a floating leaved plant as it inhabits in the fresh water such as a shallow pond with its roots spreading in the soil of the bottom and the floating leaves emerging from shoot apexes of the stems which elongate from the bottom to the surface of the water⁴⁾. It has been adapted to the environments and has rare qualities of heterocotyledon, heterophylly and heterorhizy, which have been drawing much attention in the fields of plant morphology and plant ecology. Many studies, though fragmentarily, have been conducted in terms of the anatomy, function of foliage and the root^{5, 6, 7, 8, 9, 10, 11, 12, 13)}.

But there have been few studies on the emergence and growth of organs throughout the whole growth period from germination to death of the foliage, and the formation of a floating leaf community and fruiting habit have been little known. Therefore we have to study the growth and plant morphology of the organs which compose the plant body and clarify the interrelationship between growing organs before taking up the water chestnut as a crop plant to clarify its growth response and yielding ability which are closely related to cultural control.

In this report, the time, position and order of emergence of the vegetative organs or foliage and roots of the water chestnut (*T. bispinosa* Roxb.) was clarified, and the function and role of each organ and the relation between growing organs was discussed.

Materials and Methods

Trapa bispinosa Roxb. was used as material. It was cultivated in the paddy field and water tanks. (1) Cultivation in the paddy field (transplanting culture): water tanks (60×60×50cm) with 5cm deep lowland soil were used for the raising of the seedlings. Five

germinated seeds per tank were sown on April 10, 1987. The tanks were placed in the open field to let the seedlings raised under the natural conditions. The paddy field was plowed as in the case of rice transplantation and carefully puddled in order to prevent leakage. After puddling, 2.5kg of herbicide per 10a. (Satan M-granule) was broadcasted. The paddy field was kept 10cm deep by supplying underground water. As basal dressing, 3kg of N, 3.6kg of P_2O_5 , and 3kg of K_2O per 10a were applied in the form of compound fertilizer and as topdressing, 0.5kg of N was applied in the form of ammonium sulfate on August 1 and September 1 respectively. The seedlings were transplanted on May 15. The seedlings were cut into a length of 50cm and the shoot ends of them were inserted to a depth of 10cm in the soil. The planting density was 333/10a.

(2) Tanks used for water-tank cultivation were the same type as the ones used for raising of seedlings. Four germinated seeds were sown on May 1 and periodically sampled to get a plant per tank. The tanks were kept 45cm deep by supplying city water. Fertilizer application was done as in paddy-field cultivation. The growth of seedlings using 1, 2 and 3m deep water tanks were examined.

In addition, the growth of the native *T. bispinosa* Roxb. in the Simazaki pond of Kinryuu-cho, Saga-city, was studied.

Results

The growth of hypocotyl and their branch roots

Main roots with hypocotyl, which are the organ emerging first from a germination hole, elongated toward the surface of the water. When the hypocotyl elongated about 5cm long, the cotyledon-petiole of macro-cotyledon emerged from the germination hole and elongated pushing up the hypocotyl (Fig. 1). The deeper the water depth was, the longer the cotyledon-petiole became. When the water depth became 2m or more, the cotyledon-petiole elongated more than 20cm. The hypocotyl immediately after emergence was milk-white, but when its length became a few centimeters, the color turned light green and at the same time the elongation slowed down.

The hypocotyl elongated spirally toward the surface of the water. When the length of root reached 10cm, its elongation stopped and about 150 branch roots emerged at once. The branch roots emerged on the side of the hypocotyl to form vertical rows and they elongated in all directions because of the twist of hypocotyl. The branch root had heterorhizy and developed into two different kinds of roots. One of them, emerging from the basal part of the hypocotyl, had geotropism and got

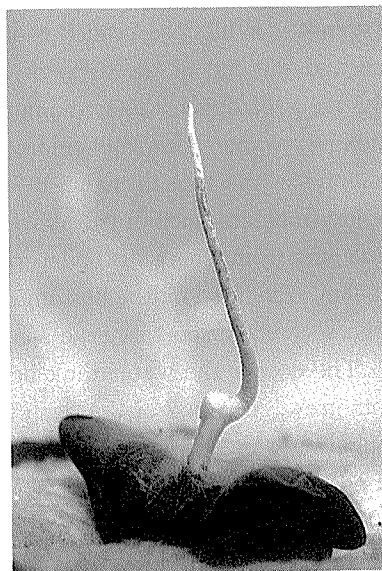


Fig. 1 Young seedlings : 9 days after germination



Fig. 2 Young seedlings : two stems emerged from coleoptyl node

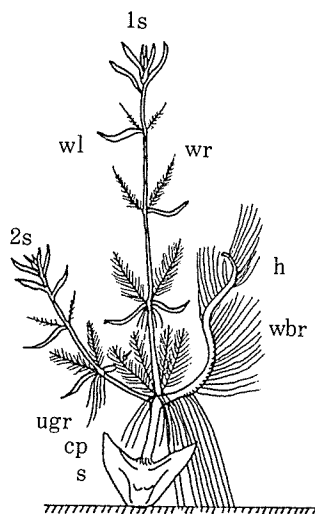


Fig. 3 Young seedling of water chestnut
1s: 1st main stem, 2s: 2nd main stem,
wl: water leaf, wr: water root, ugr:
underground root, h : hypocotyl, wbr:
water type branch root, ubr: under-
ground type branch root, cp: macro-
cotyledon petiole, s: seed.

into the soil when they reached the bottom of the water. They elongated in the soil to a length of 40-50cm, having secondary roots emerge sparsely. They elongated straight in the water but showed distinctive bendings in the soil. The part of the root in the water was brown and that in the soil was dark purple. This type of the roots is named "underground type root". While the branch roots which had emerged from the part between the basal part and the end of the hypocotyl elongated towards the surface of the water, showed negative geotropism. They did not show any bending within a length of 20cm and had few secondary roots. They had chloroplast and was light green in color. This type of the root is named "water type branch root" (Fig. 3). There emerged branches, not many, which had the intermediate form of the above-mentioned two types. They came out from almost the same part from where the underground type roots emerged. They did not get into the soil, but they elongated on the bottom of the water to a length of 20cm, brown colored and had green secondary roots emerge sparsely.

The deeper the water tank became, the longer the hypocotyl and water type branch roots grew. But in 2 or 3m deep tanks, there were some plants which had the hypocotyl elongating white without changing its color into light green. The main root of those plants did not have branch roots, corrupting and falling off along with macro-cotyledon petiole.

The emergence of main stems at cotyledon node.

The cotyledon node is at the connection of hypocotyl and macro-cotyledon petiole. On the upside of the node, there is the ligulate small-cotyledon. It grew where the macro

-cotyledon petiole stopped its elongation as it covered and protected the stem which was to emerge. First two stems emerged from where the small-cotyledon spread out (Fig. 2). It took 10 days for the stems to emerge after germination. A few days later, another two stems emerged. The stems which had emerged from the cotyledon node were to be referred as the main stems and classified as the first, second, third and the fourth main stem according to the order of their emerging so that they can be distinguished from branch stems which will be mentioned later. Each main stem had the fixed order and position of emergence from the cotyledon node. When the small-cotyledon spread out, the first main stem emerged on the side of the small cotyledon and the second one on the opposite side of the cotyledon putting the first in between. The third main stem emerged between the small-cotyledon and the first main stem 5 days after the small-cotyledon spread out. The fourth one emerged after 8 days on the opposite side of the first one putting the second one in between.

The first and the second main stems had grown as several millimeters within the small -cotyledon before they emerged. They started elongation immediately after the small -cotyledon spread out. But the third and fourth main stems had poorer incipient growth than the first and second ones, because they started growing after the small cotyledon spread out. The first main stem had a bigger diameter and elongated rapidly, but the stems that emerged later had a smaller diameter and slower growth. In addition, sometimes the fourth one did not emerge and even if it emerged, some plants stopped its development at the early stage. In 2 or 3 m deep tanks, the third and fourth stems often started elongation when the shoot apex of the first stem reached the surface of the water.

The emergence of water roots and underground roots from the base of the first main stem

Four water roots emerged from the base of the main stem 10 days after the first main stem started elongation. They are floating in the water. Three or four oblique lines of green water type branch roots which have photosynthetic ability branched from the mother root to form 3 or 4 oblique rows. The water roots emerged in the four directions with an angle of 90 degrees, surrounding the base of the first stem when the tenth leaf of the first stem came up. The number of water roots was usually four but sometimes it was three or two. The water roots at the base of the first stem emerged earlier than any other water root which emerged from the main stem. But the density of the branch roots was low and the color level was slightly lower than the water branches which emerged later.

The same type of branches, as the underground type branch roots of a main root, emerged around the water root at the base of the first main stem in a few days later than the water roots. From now on, I call the underground type branch root "underground root". The underground roots have the same form as that of the underground type branch root of a hypocotyl and showed the similar process of growth even after it got into the soil. While water roots and underground roots did not emerge from the bases of other main stems.

The emergence of organs at node

From the node which is a component of a plant body emerged a submerging or floating leaf, two water roots and more than ten underground roots. However from the first node of each main stem emerged two submerging leaves and four water roots and more than ten underground roots. Through the whole growth period, a branch bud emerged from every nodes and at the reproductive stage a floral bud emerged from every several nodes. Each organ emerged in proportion to the increasing nodes or leaf emergence, but they did not show any regular relation as seen in gramineous crop plants between leaf emergence and branching or root emergence.

The organs at the node had an approximately fixed position and direction regarding their emergence. Fig. 4 shows the view seen from right above. The node was slightly thicker than the internode at the vegetative stage. The petiole emerged from the middle of the node. The water root emerged oppositely on the both sides of the petiole. The branch-bud or floral-bud emerged from the same place of the upper part of the petiole. The underground root emerged from the surcumference of the water root. The organs emerging from the node had the fixed order of emergence in which the leaf emerged first. When the development of the leaf was stoped, the water root and the branch-bud emerged. The floral bud emerged from the same place where the branch-bud emerged. However the former was formed earlier than the latter, emerging immediately after the floating leaf spread out. The underground root emerged from the node at the later.

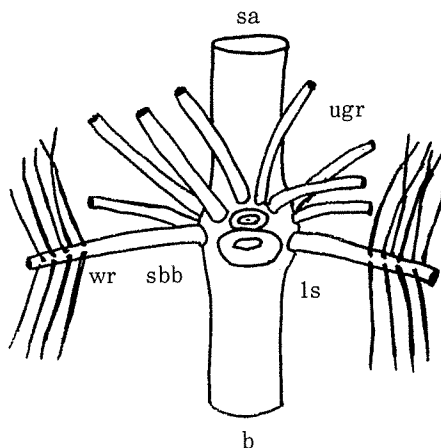


Fig. 4 Emergence of organs at node
ugr: underground root, wr: water root, ls: leaf scar, sbb: scar of branch bud, sa: shoot apex, b: base.

The elongation, thickening and branching of main stems

The stem elongated through the internode elongation. The internode which was elongated to the extent that the shoot apex reached the surface of the water showed the growth tendency of the macro-cotyledon petioles. However after the apex reached the surface of the water, only the internode a few centimeter a part from the apex elongated and the length of the internode remained almost the same regardless of the water depth. The first main stem reached the surface of the water at the earliest and the second one reached the surface a little later. The third and fourth ones, in most cases, started elongation vigorously after the first one reached the surface. Although at an early stage a slight difference could be seen in terms of the growth increment and growth rate of floating leaves, each stem which had reached the surface of the water showed almost the same process of growth.

The first main stem had 188 leaves spread out from the shoot apex at almost equal intervals from May 15 to October 25 in transplanting culture (Fig. 5). One leaf was emerged per node, so the number of the node of main stem can be considered to have increased in proportion to that of the leaves of the main stem.

The plant had slightly different leaf emergence rates according to the growing period, emerging about 1.1 leaves/day at the early stage (May and June), about 1.5 leaves/day at the middle stage (July and August) and about 0.8 leaves/day at the later stage of growth (September and November) (Fig. 6).

The internodes continued its straight elongation until the middle of August, and after that they showed little elongation. The length of main stem was 5.0m in a water-tank and 6.5m in a paddy field as of August 20. The stem was thin and weak before the flowering time, which are the typical features of the aquatic plants. However at the flowering time the shoot apex thickened rapidly to 4.0–5.0 times as thick as it was before the flowering time (Fig. 7). As mentioned above the main stem continued to have leaves emerging through out the growing period, but it had different growth types before and after the flowering time. At the vegetative stage it mainly grew elongating straight and branching and at the reproductive stage it grew thickening at the rosette part.

The main stem had the primary branched stems emerged from several nodes during the period between the apex reaching the surface of the water and flowering. And the primary branched stems had secondary and tertiary branched stems. The maximum order of branch was fifth in a paddy field and tertiary in a water tank. The branch bud emerged

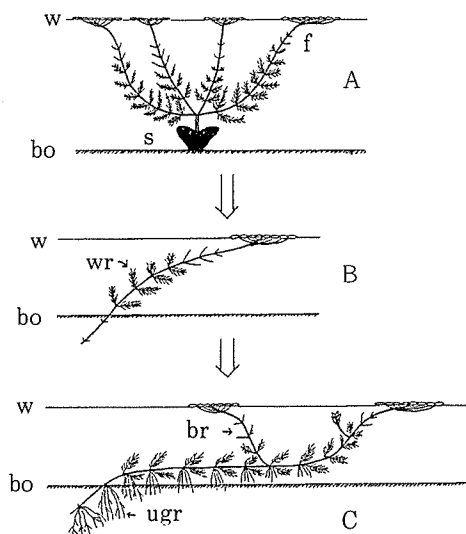


Fig. 5 Growth of one main stem after transplanting

A: raising of seedling in water tank. B: pulling of seedling and transplanting. C: growth of seedling after rooting. w: water surface, bo: bottom of water, s: seed, wr: water root, br: branched stem, ugr: underground root

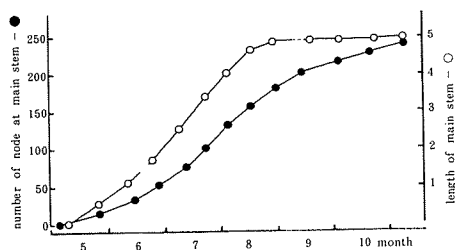


Fig. 6 Changes in number of node and length of main stem (water tank)

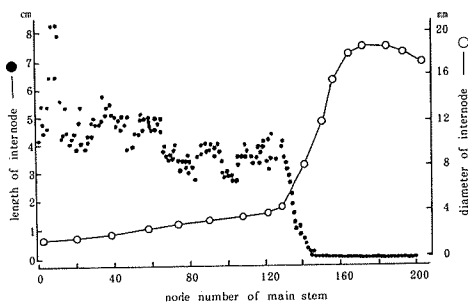


Fig. 7 Changes in length and diameter of internode

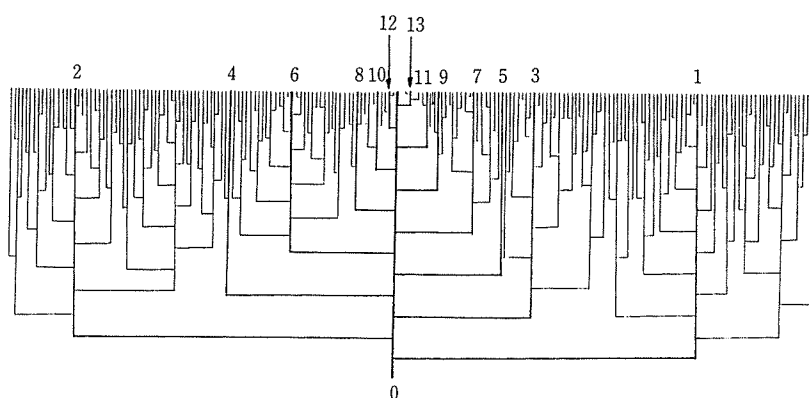


Fig. 8 Branching pattern of water chestnut (July 25, paddy field)
0: main stem, 1-13: primary branch stem.

from the node near the apex where the internode did not elongate, and the bud started its growth and elongation after the internode elongated and got off from the rosette. When the number of branch stems increased so much and they became too much dense immediately before the flowering time, small branch stems fell off.

Fig. 8 illustrates an example of branching system of average main stems which are cultivated in a paddy field. The primary branches are indicated by 0. The number of primary branched stems in the paddy field is 13, the secondary 57, the tertiary 86, the fourthly 40, the fifthly 5, that is, one main stem had 201 branch stems emerge. The number of branch stems in the tank is smaller than that in paddy field because a stem in the tank can occupy less area than the one in the paddy field.

The branch stem had the same leaf-emergence rate as the mother stem, so the branch stem had never exceeded the mother stem in growth as long as the growth of mother stem was not impeded for some reason.

The emergence of water roots and underground roots by node

Water roots emerged successively from lower node to upper nodes in line with the emergence of the leaves. The water root was smaller at an upper node than a lower node, particularly after flowering time, the mother root was shorter at a shorter internode and the same time, the number of green branch roots decreased.

Underground roots emerged successively from the node which reached the bottom of the water and got into the soil. But the underground root rarely emerged from the node with no internode elongation which was formed during reproductive period or from the node floating near the surface of the water.

The transformation of leaf form and the formation of floating leaves community

The transformation of leaf form

Leaves had heterophylly, turning into submersed leaves when in water and also turning into floating leaves with a developed aerenchyma and intercellular space after the apex of the stem reached the surface of the water. In this report, the submersed leaves are

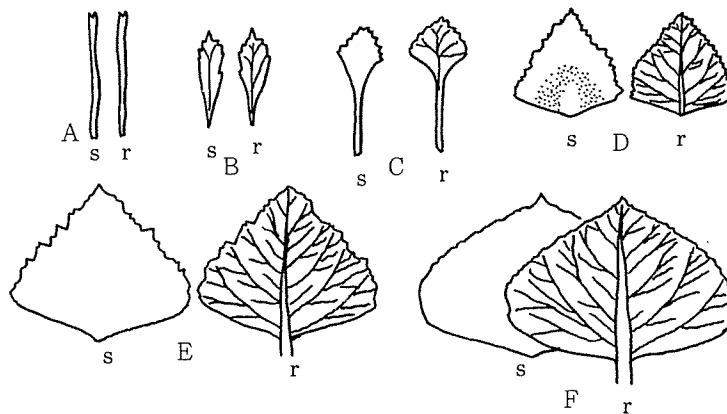


Fig. 9 Illustration of leaf blade

A: belt-shaped submerged leaf, B: submerged leaf, C: half floating leaf, D: juvenil floating leaf, E, adult floating leaf, F: emersed leaf, s: surface, r: reverse.

classified into two kinds (A, B) and the floating leaves four kinds (C; half-floating leaf, D; juvenil-floating leaf, E; adult-floating leaf, F; emersed-leaf) based on the features of the exterior morphology (Fig. 9). The leaves A to F emerged successively as the stem grew up. The submerged leaf (A) emerged when the stem apex was still deep in the water. It was an incomplete leaf without a differentiation of lamina and petiole, and belt-shaped or needle-shaped with its leaf width being almost the same from the base to apex. Another submerged leaf (B) emerged later than the submerged leaf (A) near the surface of the water and the part from middle towards the tip of the leaf blade was wider with serration. The submerged leaves (A, B) vary from light green to light brown with no luster and they fell off very soon.

The half-floating leaves are ones that emerge by only a few leaves in number in the process of the submerged leaf developing into the floating leaf, meaning that the distal end gets out of the water and turns into a floating leaf but the rest of the leaves remains in the

Table 1 Characters of floating leaf blade (Water tank)

| Item | Tentative name | Juvenil leaves | Adult leaves | Emersed leaves |
|-------------------------------|-----------------------|----------------|--------------|----------------|
| Ratio of leaf wide and length | | 0.80—0.99 | 1.00—1.35 | 1.30—1.40 |
| Leaf area | cm ² /leaf | 3.5—8.5 | 9.5—15.5 | 13.5—24.5 |
| Fresh leaf weight | mg/leaf | 110—250 | 300—550 | 500—980 |
| Dry leaf weight | mg/leaf | 22—40 | 55—95 | 120—230 |
| Number of serrate | | 20—25 | 25—30 | 30—35 |
| Leaf spot | | vivid | — | — |
| Green level | | 1.12—1.25 | 1.25—1.47 | 1.40—1.77 |
| Number of stoma | /cm ² | 18000—19000 | 20000—23000 | 25000—26000 |

Chlorophyll tester (CT-101. Fujihira. Co.) was used to measure the green level.

water and keeps the form of the submerged leaf (B). The leaves that emerged after that were all floating leaves with a petiole and blade. The blade changed its form and became larger as it grew. The blade was long lengthways at the earlier stage of the growth period, but later it changed to be long sideways. Particularly at the beginning of flowering, the leaf enlarged greatly in width and the width exceeded the length of the leaf and the ratio of leaf width and blade became bigger than 1.0. Based on the ratio of leaf width and length, the leaf was classified into two kinds. One is juvenile leaf (D) in which the ratio is less than 1.0 and the other is named adult-leaf (E) in which the ratio is more than 1.0. Another kind of leaf is named emerged leaf which has a developed petiole and blade emerged from the water. Table 1 shows the characters of the leaf blade of a juvenile leaf, an adult leaf and emerged leaf, respectively. As for the half-floating leaf, it was not compared with other floating leaves because the number of leaves was smaller and the variation of form was greater.

The leaf width to leaf blade ratio which was employed as criterion to classify floating leaves varies from 0.75 to 0.99 in juvenile leaves, 1.00 to 1.35 in adult leaves, and 1.30 to 1.40 in emerged leaves. As these figures indicate, the floating leaves were initially long lengthwise and gradually became long sidewise. The leaf margin became rounder as leaf width and blade length increased, especially emerged leaves became almost oval. The leaf area of new floating leaves continued to increase from the earlier stage of growth to the middle of September. During that period, the leaf area had closely related to the change of leaf form, and great increase in leaf area was seen in July when juvenile leaves developed into adult leaves. Floating leaves had the maximum leaf area in the middle of the September and with autumnal coolness the leaf area decreased. Leaf weight as well as leaf area increased and the adult-leaf became 2.5 times as long as the juvenile leaf and the emerged leaf was 6 times longer than the juvenile leaf. Floating leaves became greener as they enlarged. The surface of juvenile leaves were less lustrous and had brown maculae, while adult and emerged leaves were less lustrous and the maculae became less distinguishable. In the case of transplanting culture, the floating leaves of seedlings turned red after transplanting and became less greenish, but they turned green again as they used to be after taking root.

As above mentioned, the form of floating leaves changed as they grew. However emerged leaves emerged only when the surface of the water was covered with adult leaves and they did not emerged when there was space left for adult leaves to spread out.

The seasonal changes of the number and leaf area of rosette floating leaves

Floating leaves were spiral phyllotaxic, and emerged with a divergence angle of about 135 degrees, spreading out like a rosette on the surface of the water. At the vegetative stage, the internodes near the shoot apex elongated, so each floating leaf got away from the rosette and fell off as soon as the internode elongated. But at the reproductive stage, the internode stopped elongating, so floating leaves kept to the rosette until they fell off.

The number of existing leaves per rosette increased at the rate of 0.5 leaf per day from the beginning of the spreading out of floating leaves to the middle of July and reached about 40 leaves in the beginning of August. After that until the end of September, the

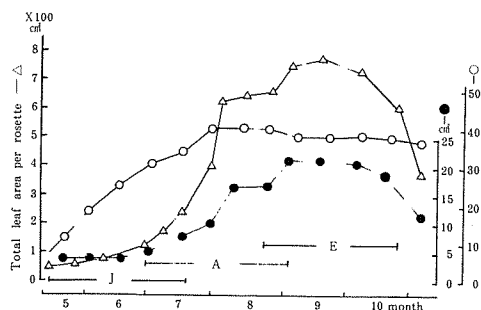


Fig. 10 Changes in leaf area of rosette floating leaves (water tank)

○—number of leaves per rosette, ●—average leaf area of individual leaf, J—emergence period of juvenil floating leaf, A—adult floating leaf, E—emersed leaf.

number of leaves remained 40 per rosette. And in October with the temperature going down, the number of leaves decreased because the defoliation rate exceeded the leaf emergence rate. In November the floating leaves seldom emerged. They died successively from older leaves and toward the end of November there was no living leaf left (Fig. 10).

The leaf area per rosette continued to increase at a slow rate until the middle July and reached 200cm. The leaf area increased rapidly from the middle of July to the beginning of August because the number of leaves as well as the single leaf area increased, exceeding 650cm at the biginning of August. During August, the number of leaves as well as the single leaf area showed little change, indicating that the leaf area per rosette remained almost the same. After that with the emergence of emersed leaves as a turning-point, it again started to increase to be 800cm and it was maintained until the end of September. But it began to decrease at the beginning of October and it amounted to less than 50 percent of its largest area in November.

The forming of floating leaf community

In the case of cultivation in a paddy field, the surface of the water was covered with floating leaves toward the end of July (Fig. 11-A). At that time, the foliage was composed of only floating leaves, with a simple structure where the leaves spread out on the surface of the water. After that period, the floating leaves began to enlarge their size as well as to increase in number to such a great extent that the density of the foliage became very high. In August the floating leaves arised from the surface of the water and the emersed leaves began to appear. Toward the end of August, almost all of the floating leaves turned into emersed leaves (Fig. 11-B). Therefore the productive structure of foliage changed its structure completely into a three-dimensional one. The emersed leaves maintained its

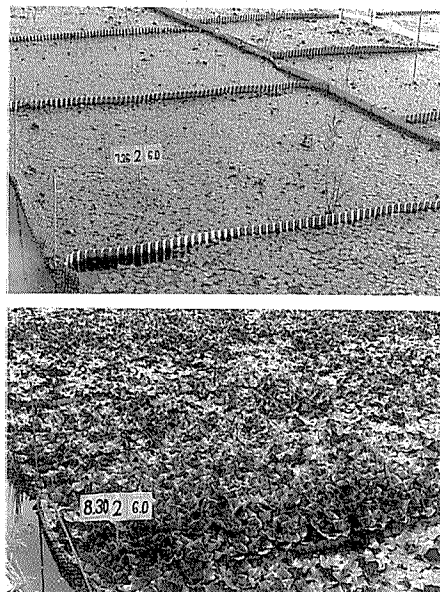


Fig. 11 Floating leaf community of water chestnut cultivated in paddy field
A: adult floating leaf community (July 26),
B: emersed leaf community (August 30)
A and B are the same experimental plot

structure until the end of September, in October the structure began to collapse through the new leaves becoming smaller and fall-off of the old leaves.

Discussion

In this study, the function and the role of organs and their adaptive system was carefully observed on the physiological and agronomical points of view, and mentioned some problems with regard to the analysis of the productive ecology of *T. bispinosa* Roxb.

The conditions for the survival of seedlings

It is imagined that the chlorosis and corrupt of hypocotyl resulted from the lack of light intensity near the bottom of the water. The condition of light at the bottom of water can be considered an important factor that controls the growth of seedlings and the elongation of the main stems toward the surface of the water. The growth of seedlings depends greatly on the reserve starch of macro-cotyledons. A study case on the relation between the consumption volume of reserve substance and the formed volume of seedlings has not been found and transformation efficiency is not well known. Therefore the morphological understanding of translocation channels from macro-cotyledon to each organ and the analysis of how water, water depth or other environmental conditions affect the transformation of reserve substance should be conducted. To elucidate the transformation system means to know the weaning stage and also supply fundamentals to know how long the stem can elongate from the bottom of the water or the water depth in which water chestnut can survive.

It is a requirement for survival that once the seedlings in the water begin to elongate, they have to have the shoot apex reach the surface of the water as soon as possible and have the floating leaves spread out. According to the observation, until the first main stem reached the surface of the water, only the water type branch roots of hypocotyl and water roots grew steadily, while other main stems and underground roots grew very slowly. This might be a proof that the water roots play the role of helping the main stem to elongate and float. Other main stems and underground roots began to grow flourishingly after the floating leaves of the first main stem spread out. A similiar phenomenon can be seen when rice seedlings are grown under anaerobic condition¹⁴⁾, so the phenomenon could be understood as resulted from the same system. This leads to the idea that the seedlings have the system where the first main stem elongates prior to other main stems and all juvenile organs collaborate to get the first main stem to reach the surface of the water as soon as possible.

The function and role of roots

ARIMA¹⁵⁾ implied that water roots have photosynthetic ability and play the role of water leaves when floating leaves are at the early stage and are not still mature, but when the floating leaves get mature, photosynthesis is conducted in the floating leaves, which makes the role played by water roots diminish. The fact that the water roots are larger

at the lower node and smaller at the higher node implies that the function and role of water roots is more important at the earlier stage. And the water roots that have emerged at the reproductive stage are considered to play little role and to be a vestigial organ.

The main function of underground roots are, judging from the form, the absorption of water and nutrition and the fixing of plant body. It is also imagined that since the underground roots emerge only near the bottom of the water and have the stems fix at the bottom successively, the underground roots play the role of not only fixing the plant body at the bottom, but also maintaining the shortest length of floating stems according to the water depth.

When the underground roots could not physically get into soil and floated in the water, or when they emerged from the nodes which were near the surface of the water, because the stem was broken off by accident, they had a lot of green water roots. The phenomenon shows the fact that the underground root has the ability of form the branch root which is adaptive to the water environments. This is very interesting from the point of view of the differentiation of functions and evolution. With regard to the origin of water root, there is an opinion that stipules evolved into water root in the process of adaptation to the water environments. But this phenomenon might support the idea that underground roots evolved into water roots^{16, 17}.

The function and role of stems

The length of internode varied according to the environmental conditions and the growth stage. The elongation of internode is similar to that of floating rice. The elongation process might be the same and be controlled by plant hormone such as gibberellin and ethylene^{18, 19}.

The role of stems is to moor the rosette and to be a supplying channel of nutrition through the whole growth period. At the vegetative stage, the stem has a function to have branch stems that have emerged successively from each node elongation and help to increase the number of rosettes. On the other hand, at the reproductive stage, the stem not only increases the buoyant force of the rosette, but also makes it possible for bigger floating leaves to emerge through the bulking of stems. And the shorter internode, meaning the shorter distance between source (floating leaves) and sink (fruits), makes the translocation of assimilation products more efficiently. As above mentioned, the stem plays different roles at the vegetative and reproductive stages respectively through changing the form. In terms of fruit production, the functions of stem was to increase the number of fruits at the vegetative stage and to help the fruits to grow at the reproductive stage.

Shoot apex continued to form nodes at regular intervals throughout its whole life. This kind of vegetative growth can be considered as a cause that the water chestnut can adapt itself to ever changing environments (weather, water depth, nutrition conditions, etc.) to a great extent, forming new practical organs and the successive leaves' reemergence maintaining the ever high-productivity.

The function and role of leaves

Water chestnut has, physiologically and ecologically, two turning-points with respect to the emergence of leaves. One is the time when the submerged leaf turns into the floating leaf and the other is when the floating leaf turns into the emerged leaf. The transformation of leaves is accompanied by the functional changes, showing the increase of photosynthetic rate and buoyancy. There are some reports that leaf-emersing results in increasing resistance against drowning and drying²⁰⁾. In this report, floating leaves are classified into four categories based on their external forms. Half-floating and emerged leaves, judging from the form, are apparently heterophyllous, but juvenil and adult leaves do not have as clear morphological differentiation as to be distinguished as heterophylly. The distinguishing criterion is whether the form of leaf blade changes from lengthways-long form to sideways-long form at about the transformation stage of growth. Many studies have been conducted on the functional differences and the system of the emergence of hetelrophlly and the system is being brought to right. The water chestnut should be also discussed on this respect^{21, 22)}.

In transplanting culture, rooting damage prevents seedlings from growing about a week immediately after transplanting. The floating leaves of seedlings turned red within a day or two and the photosynthetic rate slowed down. Few reddened leaves turned green again. The indirect cause of leaves' reddening is root and stem pruning. How it happens has not yet been examined, but it can be imagined that it results from lack of substances which translocate from roots, because when new roots emerge from the nodes and the seedlings root, the reddening get alleviated. The reddening of leaves was seen again at the later stage of growth. But this phenomenon can be thought that leaves turned red with autumal coolness due to physiological causes.

The forming of floating leaf community

In the case of common crops, the unit which composes plant community is an individual plant or a hill. Artificial population density (feeding density, planting density) is maintained until plant community has completed as long as there happens no thinning. Therefore the structure of the community can be analyzed based on an individual plant as a unit. On the other hand, water chestnut should be analyzed based on a rosette as a unit with regard to the structure and function of the community, because the water chestnut leaf comminuty is composed of rosette.

But the rosette density is quite changeable according to the enviroments or its growth stage or self thinning which results from overdensity. In addition to that the structure of the community becomes quite different from what it used to be when emerged leaves have emerged with the changing of rosette density. Therefore the analysis of floating leaf community may require more plant ecological method as well as agronomical one^{23, 24)}.

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トウビシ (*Trapa bispinosa* Roxb.) の栄養器官の生長

有馬 進・田中 典幸・窪田 文武*

(生産生物学講座)

平成元年11月11日受理

摘 要

トウビシ (*Trapa bispinosa* Roxb.) を、水田において栽培し、栄養器官すなわち茎葉および根について、その出現時期、出現位置ならびに出現順序について調査し、それぞれの器官の形状ならびに生育経過について観察した。

1. 胚軸は、螺旋状に湾曲しながら、水面に向かって伸長し、約150本の分枝根を発生させた。胚軸根系は、水深が深くなるほど、大型になった。分枝根は、異形根性を示し、胚軸基部に出現したものが底泥に貫入して、地中根となり、胚軸基部から先端にかけて出現したものが水中に浮遊する水中根となった。

2. 茎は、子葉節から4本出現した。各茎は、出現順位と出現位置が定まっていた。早く出現した茎は、後から出現した茎よりも旺盛な生育を示した。

茎は、生育期間を通じて、茎頂において一定間隔で節を形成した。節の形成速度は、生育中期(高温期)が、1日当り1.5節以上になり、生育前期と後期(低温期)が、1日当り1節以下であった。各節は、定まった位置から、1枚の葉、1対の水中根、十数本の地中根および1本の分枝芽を発生した。また、生殖生長期には数節毎に、分枝芽が変わって1個の花芽を発生させた。開花始期までに発生した分枝芽は、数節毎に生長し、水面に浮葉冠を形成した。分枝茎も母茎とまったく同じ生長経過を示した。最高分枝次位は5次まで観察された。しかし、高次分枝は、生育途中で脱落することが多かった。

茎は、開花始期を境として生育特性が異なり、栄養生長期には、伸長生長を示し、生殖生長期には肥大生長を示した。

3. 葉は、異形葉性を示し、生育時期および環境条件によって異なった形状になった。本報告ではその形態的特徴にもとづいて、水中葉を2種類、浮葉を4種類に分類した。

4. 浮葉冠は、7月下旬に最多数となり、水面を覆い尽くした。葉群落は、浮葉冠の密度が高い場合、浮葉が立葉に変化し、水面上で立体的な生産構造を形成した。

5. 生殖生長期において1つの浮葉冠は40枚前後の浮葉で構成された。浮葉冠の葉面積は、すべての葉が成浮葉になる8月中旬から、9月上旬にかけて最大になった。しかし、9月中旬から秋冷にともなって、展葉速度が低下するとともに新葉が小形化するために、葉面積は徐々に減少した。

6. 10月に入ると葉は、葉齢の進んだものから葉身が褐変して脱落し始めた。11月には、浮葉冠は消滅して、水中に茎と根が残り、まもなく、茎と根も腐敗した。

*九州大学農学部栽培学講座